

TONESTUS KINGII AND T. ABERRANS ARE RELATED TO
EURYBIA AND THE MACHAERANTHERINAE
(ASTERACEAE: ASTEREAEE) BASED ON
nrDNA (ITS AND ETS) DATA: REINSTATEMENT OF
HERRICKIA AND A NEW GENUS, TRINITEURYBIA

Luc Brouillet

Herbier Marie-Victorin
Institut de recherche en biologie végétale
Université de Montréal
4101 Sherbrooke St. E
Montréal, Québec, CANADA, H1X 2B2
luc.brouillet@umontreal.ca
(author for correspondence)

L. Urbatsch

LSU Herbarium and Biological Sci. Dept.
202 Life Sciences Bldg.
Louisiana State University
Baton Rouge, Louisiana 70803, U.S.A.
leu@lsu.edu

R.P. Roberts

LSU Herbarium and Biological Sci. Department
202 Life Sciences Bldg.
Louisiana State University
Baton Rouge, Louisiana 70803, U.S.A.
and
Department of Biological Sciences
Towson University, Towson, Maryland 21252-0001, U.S.A.

ABSTRACT

Phylogenetic analysis of nrDNA (ETS and ITS) sequence data for 50 species of Astereae (Asteraceae) belonging to the *Eurybia-Machaerantherinae* clade show that *Tonestus kingii* and *T. aberrans* belong to this group. The genus *Herrickia* is reinstated and expanded to include *H. kingii* as well as members of *Eurybia* section *Herrickia* sensu Nesom (1994). A new genus, *Triniteurybia*, is established for *T. aberrans*, which is sister to the *Machaerantherinae*.

RESUMEN

El análisis filogenético de secuencia de bases de nrDNA (ETS y ITS) de 50 especies de Astereae (Asteraceae) pertenecientes al clado *Eurybia-Machaerantherinae* muestra que *Tonestus kingii* y *T. aberrans* pertenecen a este grupo. El género *Herrickia* se reinstaura y expande para incluir a *H. kingii* así como a miembros de *Eurybia* sección *Herrickia* sensu Nesom (1994). Se establece un nuevo género, *Triniteurybia*, para *T. aberrans*, que es "sister group" de *Machaerantherinae*.

INTRODUCTION

Several species of tribe Astereae in North America have proven difficult to assign taxonomically to genera or groups. Molecular phylogenetic studies, notably following the seminal paper of Noyes and Rieseberg (1999), have helped to solve the relationships of many of these taxa. Nevertheless, the disposition of

some species still remain controversial, notably species recently included in *Tonestus* by Nesom and Morgan (1990), *T. aberrans* (A. Nelson) G.L. Nesom & Morgan (basonym *Macronema aberrans* A. Nelson), and by Nesom (1991), *T. kingii* (D.C. Eaton) G.L. Nesom (basonym *Aster kingii* D.C. Eaton). The basis for inclusion of these species in *Tonestus* were the woody caudices, leaf shape and anatomy, eglandular (or sparsely short-stipitate-glandular) herbage, mostly single-headed capitulescences and foliaceous outer phyllaries (not in *T. aberrans* however). Nesom and Morgan (1990) did not discuss the specific reasons for the inclusion of *Macronema aberrans* in *Tonestus*, but pointed out its similarities to *T. graniticus*. Nesom (1991) reviewed the detailed taxonomic history of *Aster kingii*, which has also been named *Machaeranthera kingii* (D.C. Eaton) Cronquist & Keck, and he pointed out that various authors had seen relationships of this species with genus *Aster* s.l., notably western members of *Eurybia* and *Oreostemma*. The similarities invoked to link this species to *Tonestus* are those cited above. The only discordant feature in the group would be its white rays in a yellow-rayed group. All species placed in *Tonestus* are $n=9$, a primitive and frequent number in the tribe.

A recent molecular phylogeny of *Chrysothamnus* and related *Solidagininae* (Roberts & Urbatsch 2004) suggests, however, that *Tonestus* sensu Nesom is polyphyletic. Further investigations by Urbatsch and colleagues (unpublished) suggested that *T. aberrans* and *T. kingii* might better be placed near *Eurybia*. Likewise, a study of the position of the North American asters within tribe Astereae had suggested that *T. kingii* was better placed with *Eurybia* and *Oreostemma*, two North American segregates of *Aster* s.l. (see summarized phylogeny in Semple et al. 2002) that will be called henceforth the eurybioid lineage. Therefore, in preparation for the treatment of *Eurybia* and relatives (Asteraceae, Astereae) for the Flora of North America, we are using ITS and 3'ETS molecular phylogenetic data to investigate the taxonomic position of *T. aberrans* and *T. kingii* within the Astereae. These molecular markers have proved useful in determining the position of taxa in tribe Astereae (e.g., Noyes & Rieseberg 1999; Roberts & Urbatsch 2004). We show that these species belong to the eurybioid grade within the North American clade and are presenting the necessary combinations to reflect this phylogenetic position. Genus *Herrickia* is reinstated and *T. kingii* transferred to it as *H. kingii* (along with congeners *H. glauca* and *H. wasatchensis*), and a new monotypic genus is described to accommodate *T. aberrans*, *Triniteurybia*. These names are subsequently used in the paper.

MATERIAL AND METHODS

Samples were preserved either as frozen leaf material, in silica gel, or taken from herbarium specimens. Data for the Machaerantherinae were taken from Markos

and Baldwin (2001). Extraction and molecular methods used here are as described in Roberts and Urbatsch (2004) (Urbatsch laboratory) and in Fougère-Danezan et al. (2003) (ITS, Brouillet laboratory). For ETS (Brouillet laboratory), the primers Ast-8 (Markos & Baldwin 2001) and 18S-2L (Linder et al. 2000) were used, with PCR conditions similar to ITS (above); this resulted in longer ETS sequences than those produced in the Urbatsch laboratory (*T. kingii* and *T. aberrans*).

Sequences were input into already aligned matrices of ITS and ETS for the Astereae and manually adjusted. All new sequences used in this study are deposited in GenBank under the accession numbers provided in Table 1. Sources for already published sequences are provided also.

Preliminary parsimony analyses were done on the full ITS (more than 500 taxa in Astereae) and ETS (106 taxa) matrices, using PAUP* 4.0b10 (Swofford 2002). Resulting trees (not shown) clearly indicate that *T. kingii* and *T. aberrans* are members of the *Eurybia* complex (eurybioids) at the base of the *Machaerantharinae* (see Semple et al. 2002), but the trees were unresolved (polytomy) in the current region of interest. Given that the trees were not in conflict, data were combined for 50 taxa for which both sets were available, in an attempt to better define the position of these species within the *Eurybia* complex. The total number of characters in the combined ETS + ITS matrix is 1149, of which 195 are parsimony informative; few phylogenetically informative indels are found in the reduced taxon matrix (mostly in the ITS portion) and they were not coded as distinct characters. The matrix was subjected to parsimony analysis using PAUP* 4.0b10 (TBR, characters unordered, unweighted, gaps as missing, random addition, Multrees in effect), and to Bayesian analysis using Mr.Bayes3 (Ronquist and Huelsenbeck, 2003). For the latter, the following parameters were applied: 4 chains, 1,000,000 generations, burn in 100,000, every 10,000th tree saved, model GTR+ gamma+gamma inv, nst=6. Analyses were run to completion. Bootstrap and jackknife supports were calculated for the parsimony analysis (5000 replicates, TBR, random addition); for the jackknife, 50% of characters were deleted in each run. Strict and 50% majority rule consensus trees were drawn for the parsimony analysis, and posterior probabilities were input onto the 50% majority rule tree for the Bayesian analysis. Trees were rooted using *Chloracantha spinosa* and *Canadanthus modestus*.

RESULTS

Parsimony analysis of the ETS + ITS matrix yielded 6910 trees of length 687, CI 0.662, RI 0.812 and RC 0.538. In the strict consensus tree (not shown) the eurybioids + *Machaerantharinae* form a clade, within which *Oreostemma*, *Eurybia* and *Eurybia* sect. *Herrickia* form a polytomy sister to a *T. aberrans-Machaerantharinae* clade. The parsimony 50% majority rule tree is similar to that shown for the Bayesian analysis (Fig. 1), which resulted in 9002

TABLE 1. List of voucher specimens for the sequences generated for the current study, and sources of previously published data. Current species names (e.g., Morgan & Hartman 2003)[Sida 20:1403] are used and original published names are provided in parentheses when differing (as deposited in GenBank; Markos & Baldwin 2001). For eurybioids, names proposed here are used and formerly used ones are in parentheses.

Species	Source (collectors, number, Herbarium or citation)	GenBank accession number	
		ITS	ETS
<i>Canadanthus modestus</i> (Lindl.) G.L.Nesom	Semple 10639 (WAT)	AY772432	AY772446
<i>Chloracantha spinosa</i> (Bentharn) G.L.Nesom	Spellenberg 13101 (MT)	AY772431	AY772445
<i>Oreostemma alpigenum</i> (Torr. & A.Gray) Greene var. <i>haydenii</i> (T.C.Porter) G.L.Nesom	Semple 10419 (WAT)	AY772430	AY772444
<i>Triniteurybia aberrans</i> (A. Nelson) Brouillet, Urbatsch & R.P.Roberts clone 1 (<i>Tonestus aberrans</i> (A. Nelson) G.L.Nesom & D.R.Morgan)	Urbatsch 7812 (LSU)	AY772426	AY772440
<i>Triniteurybia aberrans</i> (A. Nelson) Brouillet, G.L.Nesom & D.R.Morgan) clone 2 (<i>Tonestus aberrans</i> (A. Nelson)	Urbatsch 7812 (LSU)	AY772427	AY772441
<i>Herrickia kingii</i> (D.C. Eaton) Brouillet, Urbatsch & R.P.Roberts clone 1 (<i>Tonestus kingii</i> (D.C.Eaton) G.L.Nesom)	Garrett 1576 (US)	AY772428	AY772442
<i>Herrickia kingii</i> (D.C.Eaton) Brouillet, Urbatsch & R.P.Roberts clone 2 (<i>Tonestus kingii</i> (D.C.Eaton) G.L.Nesom)	GS.Goodrich 16357 (UT)	AY77242	AY772443
<i>Herrickia horrida</i> Wooten & Standl.	Spellenberg & Fletcher 6027 (NMC)	AY772425	AY772439
<i>Herrickia glauca</i> (Nutt.) Brouillet (<i>Eurybia glauca</i> (Nutt.) G.L.Nesom)	Semple 5758 (WAT)	AY772424	AY772438
<i>Eurybia divaricata</i> (L.) G.L.Nesom	Semple 10710 (WAT)	AY772423	AY772437
<i>Eurybia surculosa</i> (Michx.) G.L.Nesom	Semple 10527 (WAT)	AY772422	AY772436
<i>Eurybia sibirica</i> (L.) G.L.Nesom	Semple 10627 (WAT)	AY772421	AY772435
<i>Eurybia eryngiifolia</i> (Torr. & A.Gray) G.L.Nesom	Semple 10557 (WAT)	AY772420	AY772434
<i>Dieteria bigelovii</i> (A. Gray) D.R.Morgan & R.L.Hartman (<i>Machaeranthera bigelovii</i> (A.Gray) Greene)	Semple 10468 (WAT)	AY772419	AY772433

TABLE 1. continued

Species	Source (collectors, number, Herbarium or citation)	GenBank accession number	
		ITS	ETS
<i>Benitoa occidentalis</i> (H.M.Hall) D.D.Keck (<i>Lessingia occidentalis</i> (H.M.Hall) M.Lane)	Markos & Baldwin (2001)	AF251585	AF251643
<i>Haplopappus foliosus</i> DC.	Markos & Baldwin (2001)	AF251577	AF251635
<i>Haplopappus glutinosus</i> Cass.	Markos & Baldwin (2001)	AF251578	AF251636
<i>Haplopappus macrocephalus</i> (Less.) DC.	Markos & Baldwin (2001)	AF251579	AF251637
<i>Haplopappus marginalis</i> Phil.	Markos & Baldwin (2001)	AF251580	AF251638
<i>Haplopappus paucidentatus</i> Phil.	Markos & Baldwin (2001)	AF251581	AF251639
<i>Hazardia detonsa</i> (Greene) Greene	Markos & Baldwin (2001)	AF251582	AF251640
<i>Hazardia squarrosa</i> (Hook. & Arn.) Greene var. <i>grindelioides</i> (DC.) W.D.Clark	Markos & Baldwin (2001)	AF251583	AF251641
<i>Hazardia whytnei</i> (A.Gray) Greene	Markos & Baldwin (2001)	AF251584	AF251642
<i>Isocoma acradenia</i> (Greene) Greene subsp. <i>eremophila</i> (Greene) G.L.Nesom	Markos & Baldwin (2001)	AF251572	AF251630
<i>Isocoma menziesii</i> (Hook. & Arn.) G.L.Nesom var. <i>vernonioides</i> (Nutt.) G.L.Nesom	Markos & Baldwin (2001)	AF251571	AF251629
<i>Lessingia arachnoidea</i> Greene	Markos & Baldwin (2001)	AF251587	AF251645
<i>Lessingia filaginifolia</i> (Hook. & Arn.) M.A.Lane var. <i>californica</i> (DC.) M.A.Lane	Markos & Baldwin (2001)	AF251593	AF251651
<i>Lessingia filaginifolia</i> (Hook. & Arn.) M.A.Lane var. <i>filaginifolia</i>	Markos & Baldwin (2001)	AF251589	AF251647
<i>Lessingia germanorum</i> Cham.	Markos & Baldwin (2001)	AF251596	AF251654
<i>Lessingia glandulifera</i> A.Gray var. <i>glandulifera</i>	Markos & Baldwin (2001)	AF251599	AF251657
<i>Lessingia glandulifera</i> A.Gray var. <i>pectinata</i> (Greene) Jepson	Markos & Baldwin (2001)	AF251597	AF251655
<i>Lessingia glandulifera</i> A.Gray var. <i>tomentosa</i> (Greene) Ferris	Markos & Baldwin (2001)	AF251603	AF251661
<i>Lessingia hololeuca</i> Greene	Markos & Baldwin (2001)	AF251604	AF251663
<i>Lessingia lemmonii</i> A.Gray var. <i>lemmonii</i>	Markos & Baldwin (2001)	AF251606	AF251664

TABLE 1. continued

Species	Source (collectors, number,	GenBank accession number		
		Herbarium or citation)	ITS	ETS
<i>Lessingia lemmonii</i> A.Gray var. <i>peirsonii</i> (J.T.Howell) Ferris	Markos & Baldwin (2001)	AF251608	AF251666	
<i>Lessingia lemmonii</i> A.Gray var. <i>ramulosissima</i> (Nelson) Ferris	Markos & Baldwin (2001)	AF251610	AF251668	
<i>Lessingia leptoclada</i> A.Gray	Markos & Baldwin (2001)	AF251612	AF251670	
<i>Lessingia micradenia</i> Greene var. <i>glabrata</i> (D.D.Keck) Ferris	Markos & Baldwin (2001)	AF251614	AF251672	
<i>Lessingia micradenia</i> Greene var. <i>micradenia</i>	Markos & Baldwin (2001)	AF251615	AF251673	
<i>Lessingia nana</i> A.Gray	Markos & Baldwin (2001)	AF251616	AF251674	
<i>Lessingia nemaclada</i> Greene	Markos & Baldwin (2001)	AF251618	AF251676	
<i>Lessingia ramulosa</i> A.Gray	Markos & Baldwin (2001)	AF251620	AF251678	
<i>Lessingia tenuis</i> (A.Gray) Coville	Markos & Baldwin (2001)	AF251622	AF251680	
<i>Lessingia virgata</i> A.Gray	Markos & Baldwin (2001)	AF251624	AF251682	
<i>Arida parviflora</i> (A. Gray) D.R.Morgan & R.L.Hartman (<i>Machaeranthera parviflora</i> A.Gray)	Markos & Baldwin (2001)	AF251568	AF251626	
<i>Machaeranthera tanacetifolia</i> (Kunth) Nees	Markos & Baldwin (2001)	AF251567	AF251625	
<i>Pyrocoma lanceolata</i> Greene	Markos & Baldwin (2001)	AF251574	AF251632	
<i>Xanthisma spinulosum</i> (Pursh) D.R.Morgan & R.L.Hartman (<i>Machaeranthera pinnatifida</i> (Hook.) Shinners)	Markos & Baldwin (2001)	AF251569	AF251627	
<i>Xanthisma texanum</i> DC. subsp. <i>drummondii</i> (Torr. & A.Gray) Semple	Markos & Baldwin (2001)	AF251575	AF251633	
<i>Xylorhiza tortifolia</i> (Torr. & A.Gray) Greene	Markos & Baldwin (2001)	AF251570	AF251628	

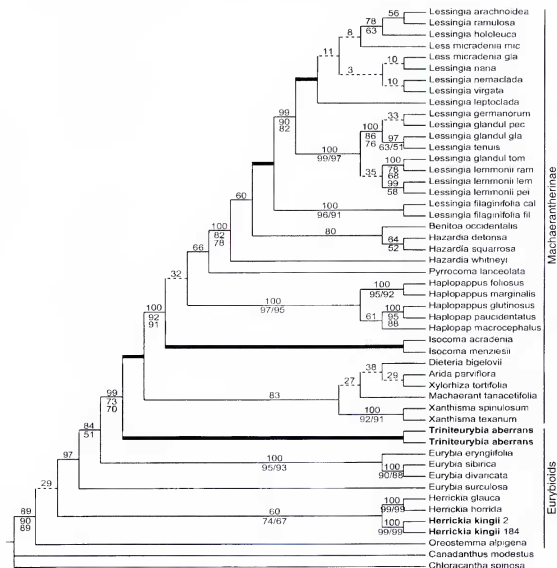


FIG. 1. 50% majority rule consensus tree of the Byaseian analysis of the eurybioids-Machaeranthrinae (Asteraceae: Astereae); *T. aberrans* and *H. kingii* are in bold; dash lines indicate branches with less than 50% posterior probabilities, thick ones those that have 100% posterior probability, 100% parsimony bootstrap and 100% jackknife support. Posterior probabilities are indicated above the lines, bootstrap and jackknife (second figure) below.

trees. Posterior probabilities are shown on Figure 1, as well as the bootstrap and jackknife support values from the parsimony analysis.

DISCUSSION

Both the preliminary separate ITS and ETS parsimony analyses and the reduced combined analyses (Fig. 1) show that *Herrickia kingii* and *Triniteurybia aberrans* belong to the eurybioid-Machaeranthrinae lineage of the Astereae. The basal branch of the eurybioid-Machaeranthrinae receives strong support (posterior probabilities 89%, bootstrap 90%, jackknife 89%), a fact further reinforced by the possession of a non-homoplastic, synapomorphic 1-bp deletion at

position 124 (ITS1). Such a relationship had been foreseen for *H. kingii* when described as a species of *Aster* s. l. (e.g., Welsh 1983) or when transferred to *Machaeranthera* section *Xylorhiza* (Cronquist and Keck 1957). Watson (1977), however, later excluded it from *Xylorhiza* when he segregated the section from *Machaeranthera*, pointing out instead similarities to *Aster* s.l. species (*Oreostemma alpigena*, *Eurybia conspicua* and *E. integrifolia*). Hartman (1990) likewise excluded *H. kingii* from *Machaeranthera*. Nesom (1991) mentioned that A. G. Jones (in pers. comm.) thought the species was associated with *Aster* sect. *Oreostemma* (*Oreostemma*), a basal group in the eurybioids. Nesom (1994), however, did not consider this possibility in his review of North American asters, though he did discuss *Tonestus* and the species studied here, noting that this (possibly polyphyletic) genus stood clearly outside *Machaerantherinae*. In transferring *H. kingii* to *Tonestus*, Nesom (1991) stressed its similarities to *T. aberrans*. A relationship to *Aster* s.l. was never envisioned for *T. aberrans*. However, the species was treated in *Macronema*, *Sideranthus* and *Haplopappus*, before its transfer to *Tonestus*, a yellow-rayed member of the *Solidagininae*, by Nesom and Morgan (1990). In all these genera, *T. aberrans* appeared unusual and aptly named.

The combined ETS + ITS analyses (Fig. 1) allow us to determine the position of *T. aberrans* and *H. kingii* within the eurybioid grade. In the parsimony strict consensus tree (not shown), the eurybioids are mostly polytomous, but *T. aberrans* emerges as sister taxon to the *Machaerantherinae*. This relationship is seen clearly in Figure 1 and receives high posterior probabilities (99%), as well as good bootstrap (73%) and jackknife (70%) support in the parsimony analysis (Fig. 1). In no analysis (Brouillet, unpublished data) is *T. aberrans* associated with *Eurybia* species. It occupies an isolated position between *Eurybia* and the *Machaerantherinae* and deserves recognition as a new monotypic genus, described below. Identification of this taxon as sister to the *Machaerantherinae* does not affect relationships previously determined within the subtribe (e.g., Morgan 2003; Markos & Baldwin 2001), and may shed light on the early evolution of this complex of mostly xeric, western species that have undergone a rapid diversification in ecology, morphology and karyology.

The position of *T. kingii* also appears resolved, but in a less striking manner. In all analyses (including a larger ITS study using different sequences for the species than those used here; Brouillet et al., in preparation), the species is sister to *Herrickia* (*Eurybia* sect. *Herrickia* of Nesom 1994; see below) (Fig. 1); it groups here with *H. glauca* and *H. horrida*, two of the three members of the genus. Support for this relationship, however, is not strong (posterior probabilities, 60%; bootstrap 74%, jackknife 67%), and is based on a single synapomorphy (in ETS) that is homoplastic due to parallel changes in the *Machaeranthera* complex. In all analyses done so far (including the large ITS parsimony study), *Herrickia* appears either in a polytomy or basal within *Eurybia* sensu Nesom

(1994). Its distinction from *Eurybia* receives 97% posterior probability, but this branch receives no support in parsimony analyses. Yet, it is defined by two synapomorphies (both from ITS1) without reversal or homoplasy. Another observation reinforces the conclusion that *Herrickia* may be best segregated from *Eurybia*, coming from cpDNA trnL-F sequence data (Brouillet, unpublished): while species of *Eurybia* s. str. have a 4-bp synapomorphic deletion, *Oreostemma*, *Herrickia*, *T. aberrans* and the *Machaerantherinae* all have the standard sequence, which suggests that *Eurybia* s. str. is a distinct clade. Despite this observation, one could advocate separating *E. surculosa* from other *Eurybia* on the basis of its position in Figure 1. The branch leading to this species is long, however. Furthermore, in analyses of ITS data using a larger set of eurybioids, *E. surculosa* groups with other *Eurybia* species, though *Eurybia* and other eurybioids globally are polytomous. The position of *E. surculosa* in the current tree appears the result of low taxon sampling and a long branch in the combined data. At the present time, relationships within and monophyly of *Eurybia* s. str. (including subgenera *Eurybia* and *Heleastrum* of Nesom 1994) cannot be tested appropriately. This is not the case for *Herrickia*, which forms a group in these analyses. Nevertheless, *Herrickia* as a genus appears monophyletic and worthy of reinstatement, with a new circumscription that includes the taxa grouped within section *Herrickia* by Nesom (1994) (i. e., *H. horrida*, *H. glauca* and *H. wasatchensis*), as well as *H. kingii*, as sister to the clade *Eurybia* s. str.-*Triniteurybia*-*Machaerantherinae*.

Herrickia Wooton & Standley, Contr. U.S. Natl. Herb. 16:186. 1913. *Eurybia* section *Herrickia* (Wooton & Standley) G.L. Nesom, Phytologia 77:258. 1994. TYPE: *Herrickia horrida* Wooton & Standley.

Herrickia horrida Wooton & Standley, Contr. U.S. Natl. Herb. 16:186. 1913. *Aster horridus* (Wooton & Standley) S.F. Blake, J. Washington Acad. Sci. 27:379. 1937. *Eurybia horrida* (Wooton & Standley) G.L. Nesom, Phytologia 77:260. 1994.

Herrickia glauca (Nutt.) Brouillet, comb. nov. BASIONYM: *Eucephalus glaucus* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:299. 1841. *Aster glaucus* (Nutt.) Torr. & A. Gray [nom. illeg.], Fl. N. Amer. 2:159. 1841 (non Nees 1818). *Eurybia glauca* (Nutt.) G.L. Nesom, Phytologia 77:260. 1994.

Herrickia glauca (Nutt.) Brouillet var. **glaucodes**. *Aster glaucodes* S.F. Blake, Proc. Biol. Soc. Washington 35:174. 1922. *Eucephalus formosus* Greene, Pittonia 4:156. 1900. *Aster glaucodes* var. *formosus* (Greene) Kittell in Tidestrom & Kittell, Fl. Ariz. & New Mexico 404. 1941.

Herrickia glauca (Nutt.) Brouillet var. **pulchra** (S.F. Blake) Brouillet, comb. nov. BASIONYM: *Aster glaucodes* S.F. Blake subsp. *pulcher* S.F. Blake, Proc. Biol. Soc. Washington 35:174. 1922. *Eurybia pulchra* (S.F. Blake) G.L. Nesom, Phytologia 77:261. 1994. *Eurybia glauca* (Nutt.) G.L. Nesom var. *pulchra* (S.F. Blake) Brouillet, Sida 20:1562. 2003.

Herrickia wasatchensis (M.E. Jones) Brouillet, comb. nov. BASIONYM: *Aster glaucus* (Nutt.) Torr. & A. Gray var. *wasatchensis* M.E. Jones, Proc. Calif. Acad. Sci., ser. 2, 5:694. 1895. *Eucephalus* Rydb., Fl. Rocky Mts. 1067. 1917. *Aster wasatchensis* (M.E. Jones) S.F. Blake, Contr. U.S. Natl. Herb. 25:557. 1925. *Eurybia wasatchensis* (M.E. Jones) G.L. Nesom, Phytologia 77:262. 1994.

Herrickia kingii (D.C. Eaton) Brouillet, Urbatsch & R.P. Roberts, comb. nov.
 BASIONYM: *Aster kingii* D.C. Eaton, Botany Fortieth Parallel 5:141 1871. *Machaeranthera kingii*
 (D.C. Eaton) Cronquist & Keck, Brittonia 9:239, 1957. *Tonestus kingii* (D.C. Eaton) G.L. Nesom,
 Phytologia 71:125, 1991.

Herrickia kingii (D.C. Eaton) Brouillet, Urbatsch & R.P. Roberts var. **kingii**.

Herrickia kingii (D.C. Eaton) Brouillet, Urbatsch & R.P. Roberts var. **barnebyana**
 (Welsh & Goodrich) Brouillet, Urbatsch & R.P. Roberts, comb. nov. BASIONYM:
Machaeranthera kingii (D.C. Eaton) Cronquist & Keck var. *barnebyana* Welsh & Goodrich,
 Brittonia 33:299, 1981. *Aster kingii* D.C. Eaton var. *barnebyana* (Welsh & Goodrich) Welsh,
 Great Basin Naturalist 43:221, 1983. *Tonestus kingii* (D.C. Eaton) G.L. Nesom var. *barnebyana*
 (Welsh & Goodrich) G.L. Nesom, Phytologia 71:125, 1991.

Triniteurybia Brouillet, Urbatsch & R.P. Roberts, gen. nov. TYPE: *Macronema aberrans*
 (A. Nelson) Brouillet, Urbatsch & R.P. Roberts

Ab *Eurybia* differt capitulae eradiatae et foliae stipitato-glandulosae. Differs from *Eurybia* by its
 eradiate capitula and stipitate-glandular leaves.

Herbs perennial, caespitose; caudices woody, ramified, from slender, creeping taproots. Stems erect, simple, slender, 0.5–2.5(–3) dm, stipitate-glandular. Leaves basal and cauline, alternate; basal mostly persistent, petiolate to subpetiolate, bases tapering, distal sessile; blades ascending, simple, obovate or oblong to broadly oblanceolate, distal usually gradually reduced, 1-nerved, margins sparsely serrate, apices obtuse to subacute, faces stipitate-glandular. Capitulescences of solitary heads or 2–4 in dense, ± corymbiform arrays, sessile or subsessile in axils of distalmost leaves. Heads discoid. Involucres cylindro-campanulate, 9–14 mm. Phyllaries in 3–4 series, imbricate, graduated, bases indurate, 1-nerved, green zones +/- basally truncate, occupying distal 1/2–1/3, apices acute, faces glandular-viscid (exposed parts). Receptacles slightly convex, alveolate, margins toothed, chartaceous, epaleate. Disc florets 25–60, bisexual, fertile; corollas yellow and often reddish (particularly in lobes), slenderly cylindric, barely ampliate, tubes shorter than throats, lobes 5, erect, lanceolate, ca. 0.8 mm, minutely and sparsely puberulent; style-branch 2–3 mm, moderately exserted, appendages linear-triangular, very acute, +/- equaling stigmatic portion, short-hairy. Cypselae fusiform, ca. 10-nerved, ca. 3 mm, faces sparsely strigillose, eglandular; pappi of few bristles in 1 series, unequal, soft, barbellate, barely exceeding disc corollas.

Etymology.—*Triniteurybia* is named for Trinity Lake, Idaho, the type locality, and the closely related genus *Eurybia*, to indicate its relationships.

The genus is known only from the Sawtooth Mountains of Idaho and the Bitterroot Mountains of Montana, where it is considered of conservation concern. It inhabits the crevices of cliffs and outcrops of the dry coniferous montane forest zone, sometimes at or above timberline. The chromosome number is yet unknown.

Triniteurybia aberrans (A. Nelson) Brouillet, Urbatsch & R.P. Roberts, comb. nov.
 BASIONYM: *Macronema aberrans* A. Nelson, Bot. Gaz. (Crawfordsville) 53:226, 1912. *Sideranthus*

aberrans (A. Nelson) Rydb., Fl. Rocky Mts. 1067. 1917. *Haplopappus aberrans* (A. Nelson) H.M. Hall, Carnegie Inst. Washington Publ. 389:185. 1928. *Tonestus aberrans* (A. Nelson) G.L. Nesom & Morgan, Phytologia 68:174–180.

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REFERENCES

- CRONQUIST, A. and D.D. KECK. 1957. A reconstitution of the genus *Machaeranthera*. *Brittonia* 9:231–239.
- FOUGÈRE-DANEZAN, M., S. MAUMONT, and A. BRUNEAU. 2003. Phylogenetic relationships in resin-producing Detarieae inferred from molecular data and preliminary results for a biogeographic hypothesis. In: B.B. Klitgaard and A. Bruneau, eds. *Advances in legume systematics, part 10, higher level systematics*. Royal Botanic Gardens, Kew. Pp. 161–180.
- HARTMAN, R.L. 1990. A conspectus of *Machaeranthera* (Asteraceae: Astereae). *Phytologia* 68:439–465.
- LINDER, C.R., L.R. GOERTZEN, B. VANDEN HEUVEL, J. FRANCISCO-ORTEGA, and R.K. JANSEN. 2000. The complete External Transcribed Spacer of 18S-26S rDNA: Amplification and phylogenetic utility at low taxonomic levels in Asteraceae and closely allied families. *Molec. Phylog. Evol.* 14:285–303.
- MARKOS, S. and B.G. BALDWIN. 2001. Higher-level relationships and major lineages of *Lessingia* (Compositae, Astereae) based on nuclear rDNA internal and external transcribed spacer (ITS and ETS) sequences. *Syst. Bot.* 26:168–183.
- MORGAN, D.R. 2003. nrDNA external transcribed spacer (ETS) sequence data, reticulate evolution, and the systematics of *Machaeranthera* (Asteraceae). *Syst. Bot.* 28:179–190.
- MORGAN, D.R. and R.L. HARTMAN. 2003. A synopsis of *Machaeranthera* (Asteraceae: Astereae), with recognition of segregate genera. *Sida* 20:1387–1416.
- NESOM, G.L. 1991. Transfer of *Aster kingii* to *Tonestus* (Asteraceae: Astereae). *Phytologia* 71:122–127.
- NESOM, G.L. 1994. Review of the taxonomy of *Aster sensu lato* (Asteraceae: Astereae) emphasizing the New World species. *Phytologia* 77:141–297.
- NESOM, G.L. and D.R. MORGAN. 1990. Reinstatement of *Tonestus* (Asteraceae: Astereae). *Phytologia* 68:174–180.
- NOYES, R.D. and L.H. RIESEBERG. 1999. ITS sequence data support a single origin for North American Astereae (Asteraceae) and reflect deep geographic divisions in *Aster s. l.* *Amer. J. Bot.* 68:398–412.
- ROBERTS, R.P. and L.E. URBATSCH. 2004. Molecular phylogeny of *Chrysothamnus* and related

- genera (Asteraceae, Astereae) based on nuclear ribosomal 3'ETS and ITS sequence data. *Syst. Bot.* 29:199–215.
- RONQUIST, F. and J.P. HUELSENBECK. 2003. Mr. Bayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- SEMPLE, J.C., S.B. HEARD, and L. BROUILLET. 2002. Cultivated and native Asters of Ontario (Compositae: Astereae): *Aster* L. (including *Asteromoea blume*, *Diplactis* Raf. and *Kalimeris* (Cass.) Cass.), *Callistephus* Cass., *Galatella* Cass., *Doellingeria* Nees, *Oclemena* E.L. Greene, *Eurybia* (Cass.) S.F. Gray, *Canadanthus* Nesom, and *Symphotrichum* Nees (including *Virgulus* Raf.). Univ. Waterloo Publ. Biol. Series 41.
- SWOFFORD, D.L. 2002. PAUP*. Phylogenetic Analysis using Parsimony (*and Other Methods). Version 4. Sunderland: Sinauer Associates.
- WATSON, T.J., JR. 1977. The taxonomy of *Xylorhiza* (Asteraceae-Astereae). *Brittonia* 29:199–216.
- WELSH, S.L. 1983. Utah flora: Compositae (Asteraceae). *Great Basin Naturalist* 43:179–357.